# Impacts of logging on density-dependent predation of dipterocarp seeds in a South East Asian rainforest

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Abstract: Much of the forest remaining in South East Asia has been selectively logged. The processes promoting species coexistence may be the key to the recovery and maintenance of diversity in these forests. One such process is the Janzen–Connell mechanism, where specialized natural enemies such as seed predators maintain diversity by inhibiting regeneration near conspecifics. In Neotropical forests, anthropogenic disturbance can disrupt the Janzen–Connell mechanism, but similar data are unavailable for South East Asia. We investigated the effects of conspecific density (two spatial scales) and distance from fruiting trees on seed and seedling survival of the canopy tree Parashorea malaanonan in unlogged and logged forests in Sabah, Malaysia. The production of mature seeds was higher in unlogged forest, perhaps because high adult densities facilitate pollination or satiate pre-dispersal predators. In both forest types, post-dispersal survival was reduced by small-scale (1 m2) conspecific density, but not by proximity to the nearest fruiting tree. Large-scale conspecific density (seeds per fruiting tree) reduced predation, probably by satiating predators. Higher seed production in unlogged forest, in combination with slightly higher survival, meant that recruitment was almost entirely limited to unlogged forest. Thus, while logging might not affect the Janzen–Connell mechanism at this site, it may influence the recruitment of particular species.

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**Title**: Impacts of logging on density dependent predation of dipterocarp seeds in a Southeast Asian rainforest

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**Abstract**

Much of the forest remaining in Southeast Asia has been selectively logged. The processes promoting species coexistence may be key to the recovery and maintenance of diversity in these forests. One such process is the Janzen-Connell mechanism, where specialised natural enemies like seed predators maintain diversity by inhibiting regeneration near conspecifics. In Neotropical forests, anthropogenic disturbance can disrupt the Janzen-Connell mechanism, but similar data are unavailable for Southeast Asia. We investigated the effects of conspecific density (two spatial scales) and distance from fruiting trees on seed and seedling survival of the canopy tree *Parashorea malaanonan* in unlogged and logged forests in Sabah, Malaysia. Production of mature seeds was higher in unlogged forest, perhaps because high adult densities facilitate pollination or satiate pre-dispersal predators. In both forest types, post-dispersal survival was reduced by small-scale (1 $m^2$) conspecific density, but not by proximity to the nearest fruiting tree. Large-scale conspecific density (seeds per fruiting tree) reduced predation, probably by satiating predators. Higher seed production in unlogged forest, in combination with slightly higher survival, meant that recruitment was almost entirely limited to unlogged forest. Thus, while logging might not affect the Janzen-Connell mechanism at this site, it may influence recruitment of particular species.

**Keywords:** Janzen-Connell hypothesis; logging; plant diversity; anthropogenic disturbance; predator satiation; secondary forest

## *Introduction*

Tropical forests are being lost and degraded at an alarming rate [1-2]. Forest loss has been particularly rapid in Southeast Asia, where less than half of the original forest cover remains [3]. While unexploited forest is now rare in the region, large areas of secondary forest remain [4-5] and their importance for conservation is increasingly recognised [6-8]. Commercial timber extraction has inevitable, dramatic impacts on the structure, diversity and community composition of these secondary forests [9-10] but they are still important reservoirs for biodiversity and provide crucial ecosystem services including provision of raw materials, soil protection and sequestrating and storing carbon [8-9, 11-12].

Despite the importance of secondary forests for species conservation, the consequences of human disturbance for the maintenance of diversity remain poorly understood [13-14]. While there is an extensive literature on the effects of human disturbance on species richness and diversity [see recent reviews in 7, 8], the effects on the structure and organisation of ecological communities and associated ecological functions and processes have received less attention [13-14]. In particular, for forest biodiversity to recover and persist following disturbances like logging, it is important that the processes responsible for maintaining diversity remain intact [14]. The mechanisms maintaining tree diversity have been extensively examined in the literature [15], and these mechanisms could be potentially disrupted by disturbance [14]. Reductions in tree diversity could have implications for diversity in other taxonomic groups because plant diversity to some extent sets the template for diversity at higher trophic levels [16-17]. A particular concern is that, even when

67 diversity is not severely reduced by exploitation itself, it might decline over time if
68 these processes have been undermined.
69
70 Much research has tried to understand the processes involved in plant species
71 coexistence, particularly in tropical forests [15]. Among the most likely candidates is
72 the Janzen-Connell mechanism [18-19], where seeds and seedlings near conspecific
73 adults or in areas of high conspecific density suffer high mortality through the activity
74 of specialised natural enemies. Consequently, locally rare species have an advantage,
75 promoting species coexistence.
76
77 Support for the Janzen-Connell mechanism mainly comes from the Neotropics, and
78 studies from Asia and Africa are rare [20]. Of the small number of studies conducted
79 in Asia, several support the Janzen-Connell mechanism [21-23] but others do not and
80 sometimes show patterns that run counter to its predictions [24-25]. The ecology of
81 Southeast Asian forests differs in several important regards from other tropical
82 regions, and so we need to be cautious when generalising from results obtained
83 elsewhere. In particular, reproduction is typically highly episodic in these forests,
84 occurring in supra-annual, community-wide mast fruiting events [26-27]. Up to 88%
85 of canopy species can fruit at the same time and the most plausible explanation for
86 this phenomenon is that it evolved to satiate seed predators [27-28]. Predator satiation
87 decreases mortality at the highest densities, directly opposing the Janzen-Connell
88 mechanism. Indeed, Janzen [18] suggested that mast fruiting species were unlikely to
89 be affected by the mechanism. However, while much of the literature on fruiting in
90 Southeast Asian forests has concentrated on mast events, there is some evidence of
91 successful recruitment outside mast events [25, 29]. In these partial fruiting episodes,

92 the chance of observing density dependence may be greater because fruiting trees are
93 relatively isolated. Seed predators may be attracted to these trees, decreasing the
94 survival of seeds close to their parent trees relative to those dispersed further away.
95
96 Deforestation and hunting may reduce seed predator populations, which may then be
97 unable to constrain the recruitment of common species. Conversely, restricting
98 predators to small forest fragments could prevent seeds of rare species from escaping
99 in space, removing the rare species advantage. Both scenarios would weaken the
100 Janzen-Connell mechanism. Studies in the Neotropics have suggested that human
101 disturbance disrupts the Janzen-Connell mechanism. Hunting and forest fragmentation
102 have both been linked to reduced density dependence and consequently plant diversity
103 [30-32]. However similar data are lacking for Southeast Asian forests, although forest
104 fragmentation and logging can reduce dipterocarp recruitment because low densities
105 of dipterocarp trees are unable to produce enough seed to satiate seed predators
106 (which are localised in remaining forest fragments)[26, 33].
107
108 In this paper we assess distance from the nearest fruiting conspecific tree (which in
109 most cases will be the parent) and conspecific density effects on survival of
110 *Parashorea malaanonan* Merr. (Dipterocarpaceae) seeds and germinating seedlings in
111 both unlogged and logged forest in Sabah, North Borneo, during a non-mast year. We
112 test the following three hypotheses:
113 1) Seed and seedling survival will increase with distance from the nearest fruiting
114 tree (distance dependence).
115 2) Seed and seedling survival will decrease with increased conspecific density
116 (negative density dependence).

3) The relationship between survival and distance and density will be stronger in the unlogged forest than in logged forest.

## Methods

*Study Site*

The study was conducted around the Danum Valley Field Centre in Sabah, Malaysian Borneo ($4^{o}58'$ N, $118^{o}48'$E). Large areas of both logged and unlogged forest lie close to the field station. The Danum Valley Conservation Area (DVCA) contains 43,800 ha of unlogged, mostly lowland dipterocarp forest. The Yayasan Sabah Forest Management Area (YSFMA) is a logging concession of almost 1 million ha.

Logging in the YSFMA began in the mid-1970s and is ongoing. The areas included in this study were logged between 1970 and 1988. Timber was extracted using a combination of high lead on steep slopes and traditional tractor-based methods in other areas. Most of the healthy stems > 60 cm diameter at breast height (dbh) were removed. Typical extraction rates were about 70 $m^3$ $ha^{-1}$ although higher rates have been reported [see 5 for further site information].

*Study Species*

*Parashorea malaanonan* is among the commonest species in the YSFMA and more widely in Sabah [5]. Permanent plots in the DVCA contain about 18.6 *P. malaanonan* stems $ha^{-1}$ [> 10 cm girth at breast height, 34]. Most of the forest in the YSFMA is classified as *Parashorea malaanonan* (Type A) forest, a category that includes much of the natural vegetation in the upper Segama region and coastal areas of Eastern Sabah [5]. *Parashorea malaanonan* is commercially harvested and its timber is

140 classed as White *Serraya* Light Hardwood [timber density 0.52 g $cm^{-1}$ [32, 35]. It is a
141 relatively fast growing dipterocarp and its seedlings perform better in gaps and
142 therefore it is considered relatively light demanding for a dipterocarp [36]. However,
143 dipterocarps in general are very shade tolerant and overall *P. malaanonan* has high
144 survival [21, 36] and growth rates [37] in understorey conditions.
145
146 *Parashorea malaanonan* appears to fruit more often than other dipterocarps at the
147 study site and successfully set seed in 1996, 2000 and 2004 [the year of this study,
148 29]. The winged seeds are dispersed by wind or gyration and mostly fall under the
149 parent tree's canopy. Several vertebrates and invertebrates have been observed
150 attacking seeds and seedlings of *P. malaanonan* including bearded pigs *Sus babatus*
151 (R. Bagchi, personal observation), rodents [38] and insect seed predators and
152 herbivores [36, 39-40].

153 *Site Selection*

154 In August 2004, fruiting *P. malaanonan* trees were located in the unlogged forest by
155 searching along trails around the field station. The logged forest was surveyed from
156 the logging roads. Ten trees were identified for the study in both forest types. Trees
157 were considered suitable if they had a large fruit crop, were >30 m away from roads
158 and >100 m from other fruiting trees included in the study. A 30 m transect was
159 established starting at the base of each selected tree. The direction of this transect was
160 constrained to avoid trails and other fruiting *P. malaanonan* trees but otherwise
161 chosen at random (i.e. a restricted random design, Fig. S1).
162

*Seedfall traps*

Traps were used to establish seedfall rates soon after the first seedfall was observed. Traps were deployed at 2 m, 10 m, 20 m and 30 m along the transects. Each 1 m x 1 m trap was constructed by suspending a piece of plastic mesh above the ground with string attached to suitable trees. Dipterocarp seeds are dispersed by gyration and generally land close to the parent tree [41-43]. Our experience is that few seeds disperse further than 30 m and this is supported by the data presented here (see Fig 1). Seeds were collected from the traps in both forests every four days between 23 September and 30 November 2004. In addition, at each census we collected five seeds (if possible) from the ground at each distance interval, but avoided the immediate vicinity of the traps and plots. These seeds would have been exposed to both pre-dispersal and post-dispersal insect predators. The collected seeds (trap and ground) were brought back to the laboratory in order to rear out insect seed predators (see *Insect Rearing*).

*Non-manipulated plots*

A 1 m x 1 m plot was established 2 m to the right of each seed trap. Seeds found in the plot were tagged with small numbered flags pinned to their wings. The presence and status of tagged seeds were checked at the same time as the seedfall traps, and new seeds were tagged and recorded. The status of each seed was recorded as potentially viable (intact seeds with no visible signs of fungal attack or insect exit holes), dead (decomposing or empty), germinated, fungus infected, insect predated (with exit holes), consumed by vertebrates (partially consumed seed remaining), seedling browsed by vertebrates or removed from the plot (presumed dead). Some of the removed seeds were possibly secondarily dispersed, but previous work on

187 dipterocarp seed predation suggests that most are consumed [25, 38]. Note that these
188 categories were not exclusive. The plots were monitored until 30 November 2004.

189 *Density manipulation plots*

190 *Parashorea malaanonan* seeds were collected from the vicinity of additional fruiting
191 trees. To manipulate density and distance independently we established two further 1
192 m x 1 m plots at distances of 2 m and 30 m from each focal tree, adjacent to the
193 existing traps, on 9 October 2004. At each distance we assigned plots to high or low
194 density treatments at random. We placed 25 (high density) or 4 (low density) tagged
195 seeds on a regular grid in the plots. The high density treatment (25 seeds $m^{-2}$)
196 corresponds to the highest density we found in the naturally-dispersed seed plots. The
197 low density treatment (4 seeds $m^{-2}$) is at the low end of seed densities observed
198 naturally and provides some within-plot replication. All naturally dispersed seeds
199 were removed throughout the experiment. These plots were censused until 30
200 November 2004, at the same time as the traps and non-manipulated plots. Seeds were
201 assigned to the same categories as those in the non-manipulated plots (see above).
202

203 *Insect rearing*

204 Seeds collected from the ground and traps in different censuses were stored separately
205 for rearing insects, but we pooled the seeds from each distance. Any visible signs of
206 insect predation were recorded and then seeds were placed in ventilated rearing boxes
207 lined with damp tissue paper. Seeds were examined every three days, and date of
208 germination or emergence of seed predators or parasitoids recorded. Lepidopteran
209 predators were pinned on emergence and dried. Emerged weevils and parasitoids were
210 stored in 90% ethanol in a freezer. After four months all seeds were dissected,

predation recorded, and any larvae or adults still inside the seeds stored in alcohol. Specimens were mounted and identified at the Natural History Museum (London) and the Oxford University Museum of Natural History. Insects were classed as pre-dispersal or post-dispersal predators on the basis of the literature [44-46]

*Statistical analysis*

We used Generalised Linear Mixed-Effects Models [GLMMs, 47, 48] for all analyses. Seedfall was modelled as a function of forest type and distance from the nearest fruiting tree, assuming a Poisson error distribution. The intercept and effect of distance were allowed to vary between trees as normally distributed random effects (random intercept and slope model).

Initial analyses suggested only small differences in survival between seeds in the manipulated and non-manipulated plots so data were combined for analyses. Seeds recorded as dead, removed or eaten by vertebrates were categorised as 'dead' while seeds in other categories were regarded as survivors. Note that seeds in the 'insect predated' and 'fungus infected' categories were not initially counted as dead, but if the seed was determined to be dead on a subsequent visit, these agents were considered responsible for their death. For each plot, the number of seeds that died or survived during each census interval was recorded.

We modelled seed and seedling survival using GLMMs, assuming a binomial error distribution. We examined the effects of forest type, distance to the nearest fruiting tree, conspecific density at the start of the census interval and the two and three-way interactions between these predictors. Total seedfall at each tree over the study was

included as a measure of medium-scale seed density. Intercept terms for each census were included in the model as normally distributed, random effects. This allows the overall survival rate to change over time (for example if older seeds or seedlings are less vulnerable), without making assumptions about the form of this relationship, similar to Cox proportional hazard models [49]. Preliminary analyses suggested that the relationship between survival and time differed considerably between the two forest types, so we included an interaction between census and forest type as a random effect. Intercept terms for trees and plots were included as normally varying random effects. The relationship between survival and time was also allowed to vary between plots as a random effect (random intercept and slope model).

The probability of predation by insects of seeds kept in the laboratory was modelled as a function of forest type and the total seed crop at each tree using a GLMM with a binomial error distribution. In a separate model, we examined the effect of distance from the nearest fruiting conspecific, forest type and their interaction using only the seeds collected from the forest floor. Predation of seeds collected in the traps will be dominated by pre-dispersal predation, and testing the effect of distance on predation of these seeds may therefore be inappropriate. In both models, separate intercepts for trees were modelled as normally distributed random effects.

There is much debate about how to appropriately test hypotheses using GLMMs [47-48]. We used the methodology recommended by Gelman and Hill [47] to construct 95% confidence intervals for parameter estimates. We resampled 1000 times from the posterior distribution of the parameter estimates, and calculated the 2.5 and 97.5% quantiles. An approximate, two-tailed, *p*-value was estimated as

$p = 1 - 2 \cdot \left| \frac{x}{1000} - 0.5 \right|$, where $x$ is the number of samples > 0. We present these approximate $p$-values and the parameter estimates on the scale of the linear predictor with their 95% confidence intervals. Analyses were executed in R 2.11.1 [50] using the add-on packages lme4 0.999375-34 and arm 1.3-05. The R-code used to fit the models is available in the electronic supplementary material.

## Results

*Seedfall*

Overall, 353 seeds were collected from seed traps in the unlogged forest and 174 seeds in the logged forest (Fig. 1a and 1b respectively). The difference was marginally non-significant (parameter estimate for the effect of logged forest $\hat{\beta}_{logged}$= -0.75, 95% confidence interval = -1.61– 0.09, $P$ = 0.076), and there was substantial variation between trees within forest types. The number of seeds in traps declined sharply with distance from focal trees, consistent with local seed dispersal (Fig. 1, $\hat{\beta}_{distance}$=-0.084, 95% CI = -0.11 – -0.06, $P$ < 0.001). Seedfall was heavy during the first few weeks of the study and began to decline after the first month of the study. Almost all seeds fell before the end of the sixth week (Fig. 1c).

----------FIGURE 1 NEAR HERE----------

----------FIGURE 2 NEAR HERE----------

*Seed survival*

Over two months, 332 seeds were naturally dispersed into the non-manipulated plots (217, 5.4 seeds $m^{-2}$, in unlogged forest, 115, 2.9 seeds $m^{-2}$, in logged forest). A further

283 1160 seeds were added to the 80 density manipulation plots (evenly distributed
284 between the two forest types). No seeds fell into 23 of the non-manipulated plots, so
285 the analyses are based on the remaining 57 non-manipulated and 80 manipulated
286 plots.
287
288 Of these seeds, 304 (38% of the non-manipulated and experimental seeds combined)
289 survived to the end of the experiment in the unlogged forest compared to 117 (17%)
290 in the logged forest. However, this difference was not significant ( $\hat{\beta}_{logged}$ = -0.29, 95%
291 CI = -2.13–1.50, $P$ = 0.746) because of the considerable variation in seed survival
292 among trees (Fig. 2a). Only seven seeds (0.2 seeds $m^{-2}$) remained in the non-
293 manipulated plots in logged forest at the end of the study compared to 75 in the
294 unlogged forest (1.9 seeds $m^{-2}$). Total seedfall at a tree had a slight positive effect on
295 seed survival ( $\hat{\beta}_{seedf\ all}$ = 0.026, 95% CI = -0.002– 0.053, $P$ = 0.072, Fig. 2b). There
296 was a strong negative relationship between small-scale density and survival in both
297 forest types ( $\hat{\beta}_{density}$ = -0.94, 95% CI = -1.31 – -0.55, $P$ < 0.001, Fig. 3). The strength
298 of this relationship was unaffected by forest type ( $\hat{\beta}_{logged:density}$ = -0.16, 95% CI = -
299 0.67 – 0.39, $P$ = 0.574). Distance from the nearest fruiting tree did not affect seed
300 survival significantly and the interaction between distance and density was also non-
301 significant (Fig. 2).
302 ----------FIGURE 3 NEAR HERE----------
303 ----------FIGURE 4 NEAR HERE----------

*Causes of mortality*

Most seed mortality appeared to be due to vertebrate seed predators, with seeds either missing or found partially eaten in the vicinity of the plots (Fig. 4). A large proportion of individuals also died soon after germinating and subsequently being browsed by mammals. Insects and fungi contributed little to the overall mortality between them. This pattern was similar in both forest types (Fig. 4).

*Insect predation*

A total of 2337 seeds were collected from the traps (566 seeds) and the ground (1771 seeds) and brought back to the laboratory. Insects (moths, weevils or parasitoids) were reared from 210 (9%) of these seeds. A higher proportion of seeds in the unlogged forest were predated (Fig. 5a, $\hat{\beta}_{logged}$ = -0.78, 95% CI = -1.16–-0.34, $P < 0.001$). Predation was reduced at trees with large seed crops ( $\hat{\beta}_{seedfall}$ = -0.01, 95% CI = -0.019 – -0.002, $P = 0.012$, Fig 5a). There was no effect of distance on predation by insects of seeds collected from the forest floor.

The most important insect seed predators of *P. malaanonan* seeds were weevils of the Anthribidae and Curculionidae (Fig. 5b, electronic supplementary material Table S1). A micro-moth from the Tortricidae (probably *Andrioplecta shoreae* Komai; K. Tuck, personal communication) was also an important pre-dispersal seed predator, accounting for all but two moths that emerged (see electronic supplementary material Table S1). When the seeds were dissected at the end of the experiment, several seeds contained dead larvae of weevils from the families Curculionidae (probably *Alcidodes* sp.) and Anthribidae (probably *Araecerus* sp.). However, no adult *Alcidodes* were successfully reared from the seeds, although a few adult *Araecerus* were. Parasitoids

were reared from 18% of predated seeds and were primarily of the families Braconidae and Ichneumonidae (Fig. 5b, electronic supplementary material Table S1). We assumed that seeds with parasitoids must have been attacked by seed predators first, and these were therefore counted as predated.

There were 41 seeds from the traps that had insect exit holes on collection, but no insects emerged from 22 of them. It is possible that these seeds had been predated by weevils of the family Nanophyidae, such as *Nanophyes* species, which often leave the seed before it falls from the tree [51].

----------FIGURE 5 NEAR HERE----------

## *Discussion*

*Effects of logging on the Janzen-Connell mechanism*

We found strong negative effects of small-scale (1 $m^2$) conspecific density on the survival of *P. malaanonan* seeds and germinating seedlings in both unlogged and logged tropical forest. The strength of this density dependence was independent of logging history. This suggests either that logging has not affected seed-predator mediated density dependence or this process has recovered within 15-35 years after logging.

Similar work in the Neotropics has generally found strong effects of human disturbance on density dependence of tree survival [30-32]. It is likely that this disparity with our data is due to differences in the type of disturbance to which the forests were subjected. While logging operations in the YSFMA extract large volumes

351 of timber, hunting pressure on wildlife is relatively low [5]. The Neotropical studies
352 compared forests subjected to intense hunting and missing key seed predators to
353 relatively undisturbed ones. Indeed, hunting was identified as the major cause of the
354 reduced density dependence in each case [30-32]. Furthermore, the Dipterocarpaceae
355 are mainly abiotically dispersed [42] in contrast to many Neotropical species that will
356 have lost dispersers as well as seed predators. Because our data are the first from
357 Southeast Asia to compare density dependent effects between unlogged and logged
358 forests, it would be premature to conclude that hunting pressure, rather than regional
359 differences, explains the differences between our results and those of previous studies.
360 However, it provides the most likely explanation. The vertebrate faunas in many
361 forests in the region suffer severely from hunting [3] so comparable data to those
362 reported here could be collected from other Southeast Asian forests.
363
364 While high conspecific density at very small scales increased mortality, seed
365 predation in the field and by insects reared in the laboratory was lower at trees with
366 large seed crops. Such positive effects of seed density are unsurprising because both
367 pre-dispersal insect [13] and post-dispersal vertebrate [52] seed predators are likely to
368 be satiated by large amounts of seeds. One explanation for the different response of
369 post-dispersal predators to density at small and large scales is that while large seed
370 crops eventually satiate them, they concentrate their foraging in areas of the seed
371 shadow with the largest seed density. Seed predation by both insects and vertebrates
372 was independent of proximity to the nearest fruiting adult, possibly because the
373 disadvantages of being close to fruiting trees are offset by the ability of large amounts
374 of seeds to satiate seed predators locally. The independence of insect seed predation to

375 distance might reflect that a large proportion of the reared insects were pre-dispersal
376 seed predators, even in the seeds collected from the forest floor.
377
378 While the strength of density dependence was very similar in unlogged and logged
379 forests, seedfall and survival rates were less so. Mean seedfall and survival were both
380 twice as high in the unlogged forest as the logged forest. Although the differences
381 between forest types in both seedfall and survival were non-significant, this reflects
382 the large amount of variation between focal trees within forest types rather than
383 similar averages. Logging, inevitably, reduces the number of adults of timber species
384 and this may explain reduced seed production in the logged forest. Increasing the
385 distance of dipterocarps to the nearest flowering conspecific reduces cross-pollination
386 and subsequently decreases seed set [25, 53-54]. Logging has been observed to reduce
387 seed production in previous work [53-54]. The seed crop in logged forest may
388 therefore be reduced at the scale of the individual tree by high proportions of
389 unpollinated and self-pollinated flowers, and at the landscape scale by a decrease in
390 the number of adult trees. Combined with the trend for survival to be highest at trees
391 with large seed crops, this led nearly all surviving seeds to be in unlogged forest. Only
392 seven seeds remained in the non-manipulated plots in logged forest at the end of the
393 study compared to 75 seeds in the unlogged forest. Thus, natural regeneration in the
394 logged forest was practically non-existent. It should be noted that even in the
395 unlogged forest, seedling densities were very low at the end of the experiment (< 2
396 seed $m^{-2}$), and may therefore make little contribution to recruitment of this species.
397
398 One caveat applies to all our comparisons between unlogged and logged forest. While
399 one of this study's strengths is that the forest types were relatively similar in

composition prior to logging [5], we only considered one area each of unlogged and logged forest. Although the replicate trees within each forest type were far from each other (> 100 m), and may be considered independent samples, the conclusions of this study apply to the forests around the DVCA and YSFMA. Furthermore, we only considered one species. *Parashorea malaanonan* is very abundant and is a relatively fast growing dipterocarp, making it an atypical species. Rarer species may be better able to escape from their natural enemies in space, and therefore show stronger distance and density dependence. Further studies at other paired areas of unlogged and logged forest, and with additional species, will be necessary to establish if the patterns discovered here apply to unlogged and logged forests in general.

*Causes of mortality*

Vertebrates caused the vast majority of the observed seed and germinating seedling mortality in the field. It has been suggested that vertebrates are unlikely to cause such density dependence because they tend to be mobile generalists [55, but see 56]. The mobility of these seed predators did not prevent them from generating strong negative density dependence in *P. malaanonan* survival. Because we did not consider heterospecifics here we cannot determine if mortality increased with conspecific density or just density in general. For the Janzen-Connell mechanism to maintain species richness, increased density of a particular species must increase predation of heterospecifics less than conspecifics [57]. It is quite possible that seeds of other species would not benefit from a rare species advantage if they had dispersed into plots with high densities of *P. malaanonan*. Other work at this site, however, suggests that small vertebrates prefer conspecific dipterocarp seeds to heterospecific dipterocarp seeds, but large, vertebrates did not discriminate between them [58].

Our field data probably underestimate insect predation of *P. malaanonan*. A proportion of insect predated seeds would have been removed from the plots (assuming vertebrates did not discriminate against them). Such seeds would have been scored as vertebrate predated, causing us to underestimate the role of invertebrates. While we examined seeds for signs of insect emergence holes, these can be easily missed in the field, especially because insects often emerge from between the wings of dipterocarp seeds. These wings are formed from the calyx and *P. malaanonan* has two long (9-16 cm) and three short (6-10 cm) wings [59]. The area between the wings is very rough and emergence holes there might be overlooked. Emergence rates from seeds kept in the laboratory provide a more realistic estimate of invertebrate attack. In the absence of vertebrate predators, insects attacked about 9% of seeds, low in comparison to other studies from the region [25, 51]. However, even our laboratory data will probably underestimate insect predation. About 54% of the seeds we collected showed evidence of insect predation but did not produce any insects and it is likely that seed predators left a proportion of these seeds before we collected them. Some weevils in the Nanophyidae have been recorded to emerge prior to seed dispersal [51]. Furthermore, much of the insect related mortality of dipterocarp seeds occurs early on in fruit development, leading to abortion. These early losses can be substantial [51], but we only started collecting seeds once they were mature, and therefore almost certainly underestimated the impact of insects.

*Mast fruiting and the Janzen-Connell mechanism*

It is generally thought that practically no dipterocarp recruitment occurs in Southeast Asian forests outside community-wide mast fruiting events [27-28]. However in this

448 study 35% of seeds in the unlogged forest and 17% in logged forest survived until the
449 end of two months. About 8% of the original seedlings in the non-manipulated plots
450 (18 individuals) were still alive in the unlogged forest sites ten months later,
451 equivalent to 0.45 seedlings $m^2$ (R. Bagchi, unpublished data). Therefore, contrary to
452 the general consensus, at least some dipterocarps recruited in a non-mast year, albeit
453 in small numbers. It is of course very possible that these individuals will die before
454 they reach maturity, or that their recruitment makes a negligible contribution to the
455 population dynamics of *P. malaanonan*. While mortality rates are very high during
456 the seed and early seedling stage described here, the seedlings that survived the
457 duration of this study will probably have to survive for several decades in order to
458 reach the canopy [42]. Without comparable data from a mast year, it is difficult to
459 determine how the density of survivors in this study compares, but it is likely to be
460 much lower than expected after a mast fruiting.
461
462 Maycock *et al*. [25] similarly reported recruitment outside major fruiting events of the
463 congeneric *Parashorea tomentella* at Sepilok Forest Reserve, another lowland forest
464 in Sabah. However, Maycock *et al.* [25] also reported negligible survival of other
465 dipterocarp species in the same fruiting event. One possible explanation could be that
466 *P. malaanonan* seeds are unpalatable. However, various seed predators (vertebrates
467 and invertebrates) have been recorded attacking *P. malaanonan* seeds and seedlings
468 [38, 40], so this seems unlikely. Maycock *et al.* [25] suggested that *P. tormentella*
469 satiated seed predators because a high proportion of trees fruited over a large area.
470 *Parashorea* species are extremely common in both Danum and Sepilok and this may
471 partly explain its success outside community-wide mast events. However, data from
472 very abundant species at other sites suggest no such pattern. Two very abundant

dipterocarp species, *Shorea lamellata* and *S. quadrinervis,* both failed to recruit after producing seeds in non-mast years [27, 60].

## Conclusion

In this study, seeds and seedlings produced during a non-mast year were predated by vertebrate predators and, to a lesser extent, insects. This predation was negatively density dependent at small spatial scales in both forest types, suggesting species diversity of logged forests will return to pre-logging levels more rapidly than might have been expected otherwise. However, survival increased with density at a larger spatial scale, probably because predators were satiated. Seed production was much lower in logged forest, and combined with the positive effects of large-scale density on survival, this resulted in recruitment being almost completely concentrated in unlogged forest. The failure of *P. malaanonan* to recruit in logged forest raises concerns about the ability of some tree species to recover from logging. If similar patterns were observed during mast years this would have serious implications for the viability of logged forests in the region. Determining if this is the case should be considered a research priority.

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**Appendices**

ESM 1: Fig S1: Layout of the study design.

ESM 2: Table S1: Families and species of insects reared from *P. malaanonan* seeds.

ESM 3: R code used to fit the models.

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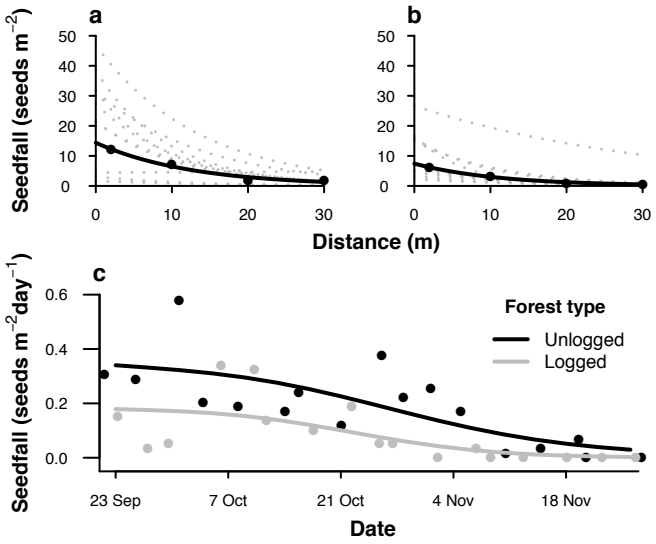
661

662 **Figures**




663

664 **Fig. 1:** The relationship between *Parashorea malaanonan* seedfall and distance from
665 the nearest fruiting tree in (a) unlogged and (b) logged forest. Points are the mean
666 number of seeds falling into 1 m$^2$ seed traps located at 2, 10, 20 and 30 meters from
667 10 trees in each forest type. Solid lines represent the number of seeds predicted to fall
668 at each distance by the model fitted to the data. Dotted lines represent the predictions
669 for each of the 10 trees in each forest type. (c) The majority of seeds fell in the first 6
670 weeks of the study. Points are the mean number of seeds that fell in seed traps placed
671 2 m away from each tree and lines are the model predictions.

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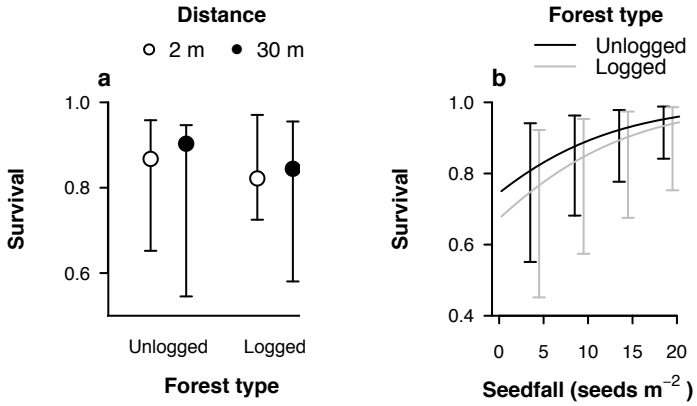


673

674 **Fig. 2:** (a) Survival of *P. malaanonan* seeds and seedlings in both unlogged and
675 logged forest. Seed and seedling survival were not significantly affected by either
676 forest type or distance from the nearest fruiting trees. (b) The effect of seed
677 production at each tree on seed and seedling survival. Data are the mean survival rates
678 (± s.e.), taking into account the variation between plots and focal trees.

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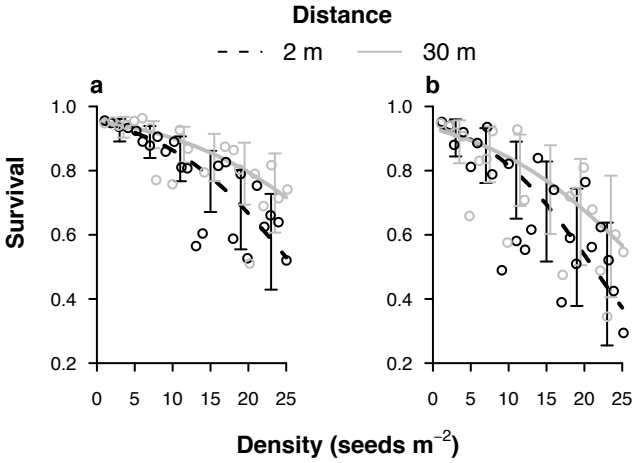
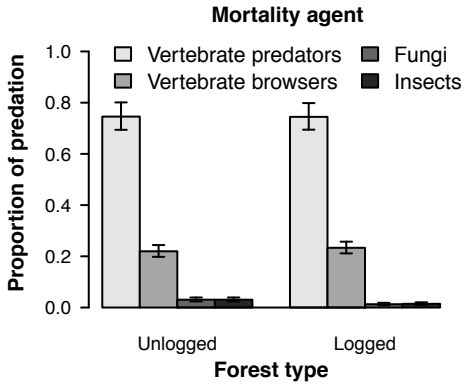



680

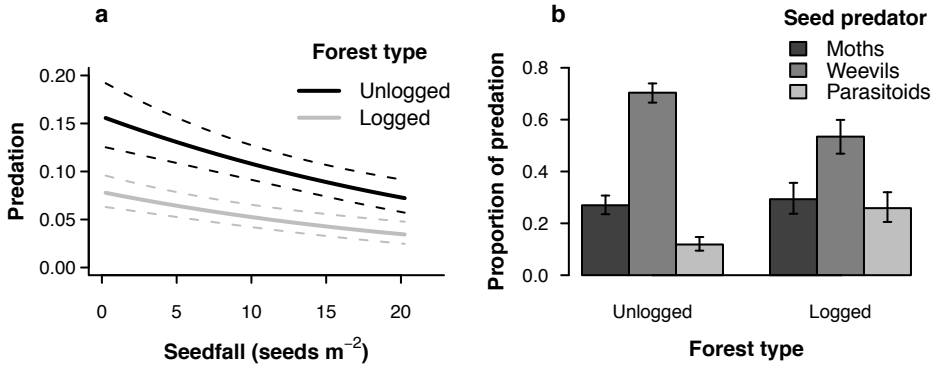
681 **Fig. 3:** Survival of *P. malaanonan* seedlings declined with conspecific seed and
682 seedling density in both (a) unlogged and (b) logged forest. Distance from nearest
683 fruiting tree did not affect survival. Points are the observed proportion of seeds that
684 survived through four-day census intervals in 1 m$^2$ plots at each density at 2 and 30 m

685 from the focal trees. Lines represent the expectations of the model fitted to the data
686 and error bars represent the standard errors.
687




688

689 **Fig. 4:** The causes of mortality of *P. malaanonan* seeds and seedlings in unlogged and
690 logged forest. Data are the mean (± s.e.) proportion of deaths in which the mortality
691 agent was implicated. Note that more than one agent could contribute to a death so the
692 proportions can add up to > 1.
693




694

695 **Fig. 5:** (a) Insect predation on *P. malaanonan* seeds collected in traps or from the
696 forest floor nearby was higher in logged forest than unlogged forest and at trees that
697 produced fewer seeds. Lines are the predictions of the models fitted to the data (±
698 s.e.). (b) The proportion of predated seeds attacked by different predators. Bars

represent the mean (± s.e.) proportion of seed predators within three different categories and the proportion of predators that had been parasitised.

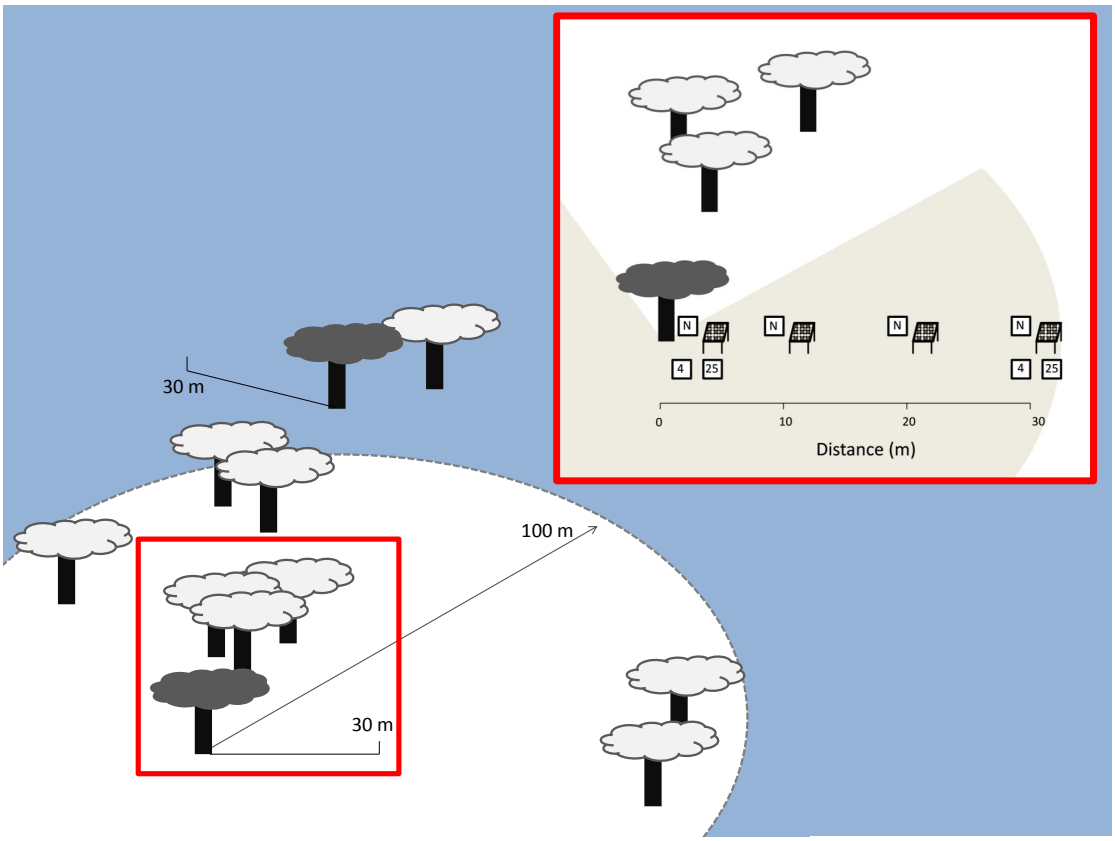



**Fig S1:** A diagram of the experimental set up at each tree. We selected 10 fruiting *P. malaanonan* trees in each forest type as focal trees. Selected trees (shaded in dark grey) were at least 100 m away from roads and other focal trees. The area shaded in white represents the area within 100 m of a focal tree. While there are other fruiting *P. malaanonan* trees (shaded in light grey) in this area, they cannot be included as independent replicates, so the nearest tree that is eligible for use as a second replicate is situated outside, in the area shaded in blue. The inset provides more detail on the design at each focal tree. We identified the directions from the focal tree for which we could set up a 30 m transect which was always closer to the focal tree than any other fruiting *P. malaanonan* (area shaded in grey). We randomly chose the transect's

713 direction from those that satisfied this criterion (i.e. a restricted random design). We
714 constructed seedfall traps at 10 m intervals along this transect, and placed 1 x 1 m
715 plots (N) beside them to monitor the survival of naturally-dispersed seeds. At each
716 end of the transect (2 m and 30 m) we marked two further 1 x 1 m plots and placed
717 either 25 (25) or 4 (4) seeds inside them on a regular grid. The plots and traps were
718 censused every four days for two months (see text for details).
719
720

**Table S1:** Families and species of insects reared from *Parashorea malaanonan* seeds. Insects were designated as pre-dispersal or post-dispersal predators on the basis of the literature (see text).

| Family | Species/Morphospecies | Predation/Host | No. of seeds |
|---|---|---|---|
| **Moths** | | | |
| Tortricidae | *Andrioplecta shoreae* Komai | predispersal | 57 |
| Pyralidae | Sp. 1 | predispersal | 1 |
| Sesiidae | Sp. 1 | predispersal | 1 |
| *Total* | | | *59* |
| **Weevils** | | | |
| Anthribidae | *Araecerus* cf. *areolatus* Pascoe adults | predispersal | 7 |
| | *Exechesops* sp. nr. *vigens* (Jordan) | predispersal | 1 |
| Nanophyidae | *Nanophyes* sp. 1 | predispersal | 4 |
| Curculionidae/Anthribidae | Unidentified larvae (possibly *Alcidodes* sp. or *Araecerus* sp.) | predispersal | 45 |
| *Total* | | | *57* |
| Curculionidae | Scolytinae unidentified species | postdispersal | 90 |
| *Total* | | | *149* |
| **Parasitoids** | | | |
| Braconidae | Sp. B1 | Pyralidae | 10 |
| | Sp. B2 | Moth? | 2 |
| | Sp. B3 | Moth? | 1 |
| | Sp. B4 | Moth? | 1 |
| Ichneumonidae | Sp. I1 | Unknown | 4 |
| | Sp. I2 | Unknown | 3 |
| | Sp. I3 | Unknown | 1 |
| Proctotrupidae | Sp. P1 | Weevil | 1 |
| Diapriidae | Sp. D1 | Diptera | 1 |
| | Sp. D2 | Diptera | 1 |
| *Total* | | | *25* |

721